Evaluation of Climate-Forced Nutrient, Phytoplankton, Zooplankton Model Output and Retrospective Estimates of Primary Production in the Hecate Strait Region 1980-2002

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EVALUATION OF CLIMATE-FORCED NUTRIENT, PHYTOPLANKTON, ZOOPLANKTON MODEL OUTPUT AND RETROSPECTIVE ESTIMATES OF PRIMARY PRODUCTION IN THE HECATE STRAIT REGION 1980-2002

by

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ABSTRACT

Ware, D., and McQueen, D. 2006. Evaluation of climate-forced Nutrient, Phytoplankton, Zooplankton model output and retrospective estimates of primary production in the Hecate Strait region 1980-2002. Can. Tech. Rep. Fish. Aquat. Sci. 2654: vii + 32 p.

This report summarizes new progress that has been made in improving the Hecate Strait nutrients, phytoplankton, zooplankton (NPZ) model and evaluating output. 1991-1999 measurements of sea surface temperature, hours of bright sunlight, alongshore wind speed, and upwelling-favourable northerly wind speed were used to calibrate two versions of the model (v4.3.3 and v4.3.4). Our goal was to determine which version produced results most closely matching available field data. In every case, v4.3.4 produced the best fits when compared with field data for algal production and zooplankton standing stocks. When model outputs were compared with 1998-1999 chlorophyll *a* concentrations measured by the SeaWiFS satellite, the resulting coefficient was $r^2 = 0.37$. When a single outlier was excluded from the data set, r^2 increased to 0.87. Our second test involved comparisons with observed anomalies in annual nestling growth rates for the Cassin's auklet population on Triangle Island. The diet of Cassin's auklet nestlings includes copepods, euphausiids, fish, carideans, amphipods and crab larvae. Growth rate anomalies were most highly correlated with the model output for the date of the spring bloom peak ($r^2 = 0.86$), and also with the modeled copepod production rates. Correlations between growth rates of Pacific herring in the Hecate Strait/Queen Charlotte Sound region and model estimates of spring zooplankton, copepod and euphausiid production produced coefficients ranging from $r^2 = 0.37$ to 0.02. Herring populations that were spatially closest to the domain of the model had the highest correlation coefficients. Finally, we assessed the possibility of using existing data for Hecate Strait phytoplankton and zooplankton to calibrate future modifications to the NPZ model. We concluded that field estimates of phytoplankton biomass were reliable enough to allow future expansion of the NPZ model to include autotrophic flagellates. However, available field-collected zooplankton data were too variable to allow meaningful tests of the model.

RÉSUMÉ

Ware, D., and McQueen, D. 2006. Evaluation of climate-forced Nutrient, Phytoplankton, Zooplankton model output and retrospective estimates of primary production in the Hecate Strait region 1980-2002. Can. Tech. Rep. Fish. Aquat. Sci. 2654: vii + 32 p.

Ce rapport résume les progrès récents en ce qui concerne l'amélioration du modèle du zooplancton, du phytoplancton et des éléments nutritifs en fonction du climat dans le détroit d'Hécate et l'évaluation des résultats de ce modèle. Nous avons utilisé les mesures de la température de l'eau en surface, des périodes d'ensoleillement, de la vitesse du vent le long des côtes et de la vitesse du vent du nord qui favorise la remontée d'eaux froides effectuées entre 1991 et 1999 pour étalonner deux versions du modèle (4.3.3 et 4.3.4). Notre objectif était de déterminer quelle version donne les résultats les plus semblables aux données obtenues sur le terrain. Dans tous les cas, la version 4.3.4 a donné les meilleurs résultats quant à la production d'algues et à la biomasse de zooplancton. Le coefficient de corrélation (r^2) entre les résultats du modèle et les mesures de la concentration de chlorophylle *a* en 1998-1999, effectuées à l'aide du satellite SeaWiFS, se chiffre à 0,37. Ce coefficient passe à 0,87 si nous excluons une seule valeur aberrante du jeu de données. Notre deuxième essai a consisté en des comparaisons avec les anomalies observées en ce qui concerne le taux de croissance annuel des oisillons de la population de stariques de Cassin de l'île Triangle. Ces oisillons se nourrissent notamment de copépodes, d'euphausiacés, de poissons, de crevettes caridéennes, d'amphipodes et de larves de crabe. Les anomalies du taux de croissance sont corrélées le plus étroitement aux résultats du modèle quant à la date du point culminant de la prolifération printanière ($r^2 = 0,86$) et au taux de production de copépodes. Les coefficients de corrélation entre le taux de croissance du hareng de la région des détroits d'Hécate et de la Reine-Charlotte et les estimations du modèle quant à la production de zooplancton printanier, de copépodes et d'euphausiacés se chiffrent entre 0,37 et 0,02. Les coefficients de corrélation les plus élevés ont été obtenus pour les populations de harengs les plus près de la région couverte par le modèle. Finalement, nous avons évalué la possibilité d'utiliser les données existantes sur le plancton du détroit d'Hécate pour étalonner les modifications futures à apporter au modèle. Nous concluons que les estimations sur le terrain de la biomasse de phytoplancton sont suffisamment fiables pour permettre l'élargissement du modèle afin qu'il tienne compte des flagellés autotrophes. Les données sur le zooplancton recueillies sur le terrain sont cependant trop variables pour permettre la réalisation d'essais concluants du modèle.

INTRODUCTION

This report summarizes new progress that has been made in improving the Hecate Strait Nutrient, Phytoplankton, Zooplankton (NPZ) model and evaluating the output of the model. We also outline some new analyses that we have conducted to assess autotrophic flagellate and diatom abundance, and zooplankton biomass in Hecate Strait.

METHODS

Wind Mixing (Model v4.3.4)

The structure of a climate-forced Nutrient, Phytoplankton, Zooplankton model developed for the Hecate Strait Region has been described by Ware and McQueen (2006). In an earlier version of the model (v4.3.3), *new* nitrogen was added to the photic zone exclusively by winter wind mixing (which determined the nitrogen concentration in the photic zone at the beginning of the production season), and by upwelling. *Regenerated* nitrogen was also added by zooplankton and fish excretion. In the newest version of the model (v4.3.4), another source of new nitrogen is added to the photic zone by spring, summer and fall wind mixing (hereafter called *seasonal wind mixing* for simplicity). Measurements in Hecate Strait indicate that phytoplankton rapidly deplete nitrogen in the top 20 m of the photic zone during the production season (Denman *et al* 1985). The nitrogen concentration below 20 m increases non-linearly to a value of about 30 mmol $NO_3 \cdot m^{-3}$ at 200 m depth (Fig. 1). From these data we calculate that the nitrate concentration (mg $NO_3 \cdot m^{-3}$) increases with depth roughly as follows:

$$NO_3 = 14 * 1.32(\text{Depth} - 20)^{0.612}$$

where n = 175 and $r^2 = 0.88$. Conceptually, we assume in the model that after a strong wind mixing event occurs, NO_3 is distributed uniformly from the surface to the depth of mixing (MD, in metres). As a rough approximation, we calculate that the amount of new nitrogen (mg $NO_3 \cdot m^{-3}$) added to the photic zone by this event can be described by:

$$N_{Mixing} = [0.5(MD-20) * 14 * 1.32(MD-20)^{0.612}]/MD$$

For example, if the mixing depth during a strong mixing event is 40 m, then after the event, the average NO_3 concentration in the top 40 m is about 29 mg $NO_3 \cdot m^{-3}$. Although the preceding formula tends to slightly underestimate the average NO_3 concentration, given all the uncertainties involved, our estimate of N_{Mixing} is probably accurate enough.

Figure 2 shows the cumulative amount of nitrogen added to the photic zone by seasonal wind mixing, upwelling, and regeneration processes during 1992. We estimate that due to winter wind mixing, the concentration of new nitrogen

(mg $NO_3 \cdot m^{-3}$) in the photic zone at the beginning of the production season (1 March) was 280 mg $NO_3 \cdot m^{-3}$ (26% of the total amount of nitrogen available to phytoplankton). Upwelling added another 462 mg $NO_3 \cdot m^{-3}$ (43% of total), while seasonal wind mixing added 146 mg $NO_3 \cdot m^{-3}$ (13% of total). Accordingly, we estimate that wind mixing and upwelling added 888 mg $NO_3 \cdot m^{-3}$ of new nitrogen to the photic zone in 1992, while regeneration processes added another 189 mg $N \cdot m^{-3}$ (18% of total) for a total of 1077 mg $N \cdot m^{-3}$. Thus the f-ratio, which is defined as the ratio of new nitrate-based primary production to total primary production in 1992 was probably about 0.82 (888 mg $N \cdot m^{-3}$/1077 mg $N \cdot m^{-3}$) in the Hecate Strait region. Assuming that all of the nitrogen in the photic zone, which has an average depth of 30 m, is converted to carbon by phytoplankton, and using a typical phytoplankton carbon/nitrogen ratio of 6.5, our model suggests that the depth-integrated *gross rate* of primary production in 1992 was probably about 210 g $C \cdot m^{-2}$, while the *net rate* was about 193 g $C \cdot m^{-2}$.

Table 1 summarizes the cumulative amount of nitrogen added to the photic zone by winter wind mixing, seasonal wind mixing, upwelling, and regeneration processes. This table highlights the importance of seasonal wind mixing which occurs primarily in the spring and fall, and upwelling as sources of new nitrogen. The former process contributed more nitrogen in 4 of the 9 years, while upwelling contributed more in another 4 of those 9 years. Both processes contributed about equal amounts in 1994. Note that the highest amount of total nitrogen (new + regenerated) was added to the photic zone in 1991.

RESULTS and DISCUSSION

Retrospective Estimates of Primary Production 1991-1999

Measurements of sea surface temperature (°C), hours of bright sunlight, alongshore wind speed ($m \cdot s^{-1}$), and upwelling-favourable northerly wind speed ($m \cdot s^{-1}$), are available from moored meteorological buoys in the area and at nearby coastal weather stations. Daily time series of these data currently extend from 1991 to 1999. We used these data to force both versions of the model (v4.3.3 and v4.3.4) and estimated the resulting primary and zooplankton production. Table 2 summarizes the number of major wind mixing events during the spring, the date when the spring bloom peaked, and the cumulative fraction of the primary production (ecotrophic coefficient) that was grazed by zooplankton according to Model v4.3.4.

A major wind mixing event was considered to have occurred when the depth of mixing was greater than 50 m. Note that the spring bloom peaks later during springs which have a high number of strong mixing events. The last column of Table 2 shows that the fraction of primary production grazed by zooplankton varies around 44-53%.

Additional diagnostic results for both versions of the model are summarized in Tables 3 and 4. These results indicate that Version 4.3.4 of the model produces

higher estimates of primary production and zooplankton production, particularly in 1997 and 1999 (Fig. 3). Model v4.3.4 includes an additional source of new nitrogen from wind mixing during the spring and fall compared to the earlier version.

Model Evaluation

At this point we don't know which version of the model produces more reasonable estimates of primary and zooplankton production. To determine this, we assembled three proxy records of lower trophic level production in the Region and examined the correlation between these indices and the output from both models.

The first proxy indicator is the average monthly surface chlorophyll *a* (chl *a*) concentration measured by the SeaWiFS satellite. The available data will only allow a comparison for 1998 and 1999. The data are shown in Table 5.

It is too much to expect a 1:1 correspondence between the observed and estimated surface chl *a* concentrations since we don't know the carbon to chl *a* ratio or how the ratio of surface to average chl *a* in the water column changes over time. In the latter case, we have assumed a constant ratio in the model (0.39), which Table 5 suggests may be too high most of the time. This ratio has no effect on the model estimates of primary and secondary production. All it does is scale the surface chl *a* up or down relative to the average chl *a* concentration in the photic zone. Consequently, what we are looking for is the best correlation in the observed time-evolving *pattern* in surface chl *a* measured by the satellite and estimated by the model. In 1998, the output from both models had the same degree of correlation with the measured values (v4.3.3 $r^2 = 0.18$; v4.3.4 $r^2 = 0.18$). However, in 1999 v4.3.4 yielded a much higher correlation (v4.3.3 $r^2 = -0.02$; v4.3.4 $r^2 = 0.37$; Fig. 4). From this we conclude that the primary production dynamics captured by v4.3.4 of the model appear to provide a better match to the observed data. Indeed, if the data point for September 1999 in Figure 4 is excluded as an outlier, the resulting correlation is quite remarkable ($n = 6$; $r^2 = 0.86$; $p = 0.008$).

For a second proxy indicator of production in the Region we use the observed anomalies in annual nestling growth rates for the Cassin's auklet population on Triangle Island (Bertram *et al* 2001). Cassin's auklet is a small planktivorous burrow-nesting seabird that breeds in May. The observed hatch date ranged from 18 May (1994) to 29 May (1999). The diet of Cassin's auklet nestlings includes copepods, euphausiids, fish, carideans, amphipods and crab larvae. Copepods were the primary prey and were dominated by a single species *Neocalanus cristatus*, copepodite stage C5. The life cycle of this species is strongly seasonal, involving a relatively brief spring and early summer growth season spent in the upper 100 m. By the end of its growing season *Neocalanus cristatus* accumulates substantial lipid reserves and then undertakes an ontogenetic vertical migration which includes prolonged periods of dormancy, delayed maturation, and spawning at depths ranging between 400-2000 m (Bertram *et al* 2001). Field studies indicated that copepods were more abundant in the nestling diet in 1997 and 1999. Bertram *et al* (2001)

found that low growth rates of Cassin's auklet occurred when copepod composition in nestling diet was low overall and copepods were scarce or absent in samples collected later in the season. Nestling growth rate data overlap with output data from our model for the period 1994-1999 (Table 6).

A correlation analysis indicated that the growth rate anomalies were most highly correlated with the date of the spring bloom peak estimated by model v4.3.4 ($r^2 = 0.86$; Fig. 5), and also with the copepod production rates estimated by the same model. The correlations with the output from v4.3.3 were consistently much poorer. From this we conclude that the dynamics captured by model v4.3.4 are more highly correlated with the growth anomalies of Cassin's auklet nestlings.

We presume that the striking correlation with the date of the spring bloom peak indicates that nestling growth rates are high when the spring bloom peaks later in the season. In contrast, when the spring bloom peaks early, presumably *Neocalanus cristatus* will complete its growth cycle and begin migrating to depth much earlier than usual. An earlier onset of the *Neocalanus cristatus* migration decreases the availability of this species to foraging Cassin's auklet adults. Consequently, the results shown in Fig. 5 support Bertram *et al*'s (2001) conclusion that when the spring is early and warm, the duration of overlap of seabird breeding and copepod availability in surface waters becomes reduced, effectively creating a seasonal mismatch of prey and predator populations.

The third proxy indicator is the growth rates of Pacific herring (*Clupea harengus pallasi*) in the Hecate Strait/Queen Charlotte Sound region. Pacific herring is a planktivorous species that forages on a wide range of planktonic zooplankton species. The average annual growth rates of Central Coast, Queen Charlotte Islands and Prince Rupert District herring (ages 3 to 6) were expressed as population specific growth rates, defined as:

$$PSG = EXP(G_{jt})$$

where G_{jt} is the mean annual instantaneous growth rate for ages 3 to 6 in population j in year t. Table 7 summarizes the estimated growth rates for the three herring populations.

The correlations between these growth rates and model estimates of "spring" zooplankton, copepod, and euphausiid production were determined (Table 8). The results indicate that the growth rate of the east coast QCI herring population, which is the closest spatially to the domain of the model, is consistently the most highly correlated with the Model v4.3.4 estimates of primary and secondary production (Fig. 6). The other populations which are further away geographically have weaker positive correlations, or even negative correlations.

Relationship Between Primary Production and Upwelling

The results of the preceding section indicate that model v4.3.4 appears to produce *consistently* better estimates of primary and secondary production. Accordingly, we will focus the rest of our analysis on the output from this model. Figure 7 shows that there is a highly significant positive relationship between the average upwelling-favourable (i.e. northerly) alongshore wind speed during the production season (1 March to 30 November) and the primary production estimated by model v4.3.4 during the period 1991-1999. Thus, given a reasonably accurate alongshore wind speed time series we can use this relationship to obtain a rough, retrospective estimate of the annual primary production in the Region.

Alongshore Wind Speed Time Series

We obtained a daily upwelling time series from the Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/) for a station at latitude 51°N longitude 131°W, which is about 60 nautical miles south and 45 nautical miles seaward of the model domain (Buoy 46185). The time series contains daily estimates of upwelling ($m^3 \cdot s^{-1} \cdot 100$ m coastline^{-1}) from 1 January 1967 to 31 December 2002. We calculated the daily geostrophic alongshore wind speed ($m \cdot s^{-1}$) from these data for the period 1 January 1980 to 31 December 2002. A comparison between the estimated alongshore northerly geostrophic winds and the measured northerly wind speed at Buoy 46185 for 1992 indicated that there was a highly significant positive correlation between the measured and the geostrophic winds (Fig. 7). A comparison of the geostrophic and the measured upwelling-favourable wind speed from 1991-1999 indicated that, on average, the geostrophic mean wind speed (1.82 $m \cdot s^{-1}$) was about 9% lower than the measured wind speed (1.99 $m \cdot s^{-1}$) in Hecate Strait. Despite this slight offset, Figure 8 substantiates that the geostrophic wind speed time series provides a fairly accurate estimate of the upwelling-favorable alongshore wind speed at the location of Buoy 46185.

Retrospective Estimates of Primary Production 1980-2002

Using the annual average upwelling-favourable wind speed (UWind) record described in the following section, we computed the regression between the estimated UWind data and the Model v4.3.4 estimates of primary production for 1991 to 1998. The resulting equation is:

$$\text{Primary Production} = 48.94 * \text{UWind} + 91.4$$

where $n = 9$, $r^2 = 0.38$, and $p = 0.07$. We used this equation and the estimated UWind values listed in Table 9 to estimate the primary production for the period 1980-2002 (Fig. 8).

The results suggest that the most productive years in the time series were 1980, 1982, 1985, 1992, 1998, and 2002. The least productive years were 1983, 1984,

1988, and 1997 (Fig. 9). Figure 10 highlights the decadal trend in the primary production time series. It suggests that production tended to be low in the early 1980s, but then increased up to the end of the record in 2002.

Figure 11 shows how well the retrospective primary production estimates match the Model v4.3.4 estimates.

Relative Abundances of Diatoms and Flagellates

The objective of this section is to determine whether it will be possible to use existing data for Hecate Strait phytoplankton to calibrate future modifications to the Hecate Strait NPZ model. The current version of the model includes five dynamic pools (nitrogen, phytoplankton, "spring" zooplankton, copepods, and euphausiids). Based on research in other ecosystems, it seems likely that model estimates of the production of the different groups of zooplankton could be improved by adding a simplified microbial food web. Specifically, this would involve splitting the existing phytoplankton group into an autotrophic nanoplankton pool (i.e. flagellates) and a diatom pool. We would also add bacteria and microzooplankton. By expanding the model in this direction, we would be able to: 1) estimate how much primary production flows through the microbial food web, creating a longer food-chain and a less efficient transfer of energy to higher trophic levels; and 2) investigate how much primary production flows directly to the zooplankton consumed by fish species in the ECOSIM model. Estimates for other coastal marine ecosystems suggest that, on average, only 45% of the total primary production is available to mesozooplankton (ecotrophic efficiency); the rest is consumed by the microbial food web. By adding a microbial food web to the model we would be able to estimate the zooplankton ecotrophic coefficient for the Hecate Strait region, and evaluate how much it may have changed in response to the natural climate variability that occurred during the 1990s. So the question is, how comprehensive are existing Hecate Strait phytoplankton data and can these data be used to guide the development of an expanded NPZ model?

Available Hecate Strait phytoplankton data and field measurements of chlorophyll *a* data are based on data from two published sources based on the Ships-of-Opportunity Program (Dilke *et al* 1979; Perry *et al* 1981) where the focus was on annual abundance patterns in diatom and flagellate phytoplankton. Dilke *et al*'s (1979) samples were collected during 7 cruises from 13 March 1978 through 8 April 1979. The Perry *et al* (1981) samples were collected during 8 cruises from 8 May 1979 through 7 June 1980. Data are available as downloadable Excel spreadsheets (*Dilke et al 1979 chla phyto.xls*; *Perry et al 1981 chla phyto.xls*; see Appendix B).

The same method of sample collection was used by both Dilke *et al* (1979) and Perry *et al* (1981). Seawater samples for the analysis of nutrients, chlorophyll *a* and phytoplankton where taken from a depth of 3 m using the ship's water intake. The water was pumped from the sea-chest through a Jabsco impeller pump and the sample was integrated over the length of the sampling transect (usually 1.3 km for

Dilke *et al* 1979, and over 1.3 km for Perry *et al* 1981). Chlorophyll *a* samples were obtained from 200 mL of seawater filtered through Watman GF/C filters which were then frozen. Chlorophyll and phaeopigments were determined by fluorometric techniques following the methods of Yentsch and Menzel (1963). Algal counts were based on 240-mL samples preserved in Lugol's solution. Settled volumes were assessed using an inverted microscope (Utermöhl 1958). Typically, 10-100 mL of each sample was settled and subsampled.

Data from the preceding two sources were combined and analyzed. The main findings were:

1. Not surprisingly, there was a positive log-log relationship between cell counts and chlorophyll *a* (Fig. 12). Also the pennate diatoms accounted for most of the chlorophyll (and probably most of the cell biomass).

2. Chlorophyll *a* plotted with respect to month showed the expected pattern of low chlorophyll concentrations in the winter and higher concentrations in the spring and summer (Fig. 13).

3. This was also seen for cell counts plotted with respect to month (Fig. 14).

4. In terms of total cell counts, flagellates were much more abundant (two orders of magnitude) than diatoms (Fig. 14). However diatoms are much larger and therefore probably account for most chlorophyll *a*.

5. Total flagellate counts were more variable during the summer (Fig. 15).

6. Diatoms generally comprised a larger proportion of the cell counts in the spring and summer (Fig. 16).

The objective of the foregoing analysis was to see if existing Hecate Strait phytoplankton data could be used to calibrate future modifications to the NPZ model. The answer is probably "yes". Even though the data set is relatively small (n = 51), there is a clear summer-winter trend, and there are quite clear differences in the abundances of diatoms and flagellates (Fig. 14). When combined with detailed data from other sources for nearby locations (i.e. Ziemann and Fulton-Bennett 1990), it should be possible to usefully expand the NPZ model to include autotrophic flagellates.

Hecate Strait Zooplankton Update

In March 2001, a report titled "Handbook of physical, chemical, phytoplankton and zooplankton data from Hecate Strait, Dixon Entrance, Goose Island Bank and Queen Charlotte Sound" (McQueen and Ware 2006) was prepared for the DFO project: "An Ecosystem Approach to Fisheries Management in Hecate Strait", Pacific Biological Station, Nanaimo, BC. The zooplankton data sets used in that

report were complete to part-way through 2001. Data are now available for all of 2001 and 2002, so the first objective of this section is to update the data set available for Hecate Strait and Queen Charlotte Sound.

The second objective is to use this expanded data set to test the hypothesis that the inter-annual zooplankton patterns produced by the NPZ model can be compared to the inter-annual patterns found in the field data.

Treatment of the zooplankton data set used here is somewhat different from the treatment used in the 2005 report. The differences are that: 1) the new data set is larger (n = 244 samples); 2) it includes only spring and summer data (March – October); and 3) for all taxa except euphausiids, the night and day data have been shown to be statistically the same and therefore night and day data are used interchangeably. However, in the case of euphausiids, a night/day correction has been applied to scale the day data up to the levels observed at night. The new data set includes samples from 1990 to 2002. Finally, the new data set includes data from Hecate Strait and Queen Charlotte Sound, but does not include data from Dixon Entrance (see Appendix B instructions to download "*Zooplankton Hecate QCS.xls*").

The methods used to scale the euphausiids are based on an IOS-funded study involving all available zooplankton samples (n ≈ 2000) collected over all of the Canadian Pacific Coastal Shelf. The processing methods used for these data involve five steps:

1. All the data from the BC Coastal Shelf were combined into one large file. The data were then sorted (in several steps) into night and day data.

2. The 53 zooplankton groups are combined into 12 groups as shown in Ware and McQueen (2006). For each of the 12 zooplankton groups we used ANOVA to test the hypothesis that the night and day mean biomasses were the same. To do this, we first removed the effects of dusk and dawn by removing all of the samples collected between 05:00-07:00 and 20:00-22:00. We then did our ANOVA analysis on the remaining data and found no significant effect of diel migration except for the 2 euphausiid groups. For *E. pacifica* we found that the night biomasses were 2.8 times higher than the day biomasses, and for *Thysanoessa* species we found that night biomasses were 5.35 times greater. Therefore we added the dawn dusk data back into the data set and applied the day correction (multiplied the day data by the correction factors) to the two euphausiid groups. Day was defined as 06:00-21:00 and night as 21:01-05:59.

3. Day-night corrections were applied to the euphausiids and ANOVA were run for the day-night data for all groups to be sure that the day and night mean biomasses were not different. No differences were noted.

4. The corrected data were re-sorted for area (11 areas) and then the Hecate Strait and QCS values were extracted for Step 5.

5. These data are summarized for a number of important zooplankton groups in Table 10.

In accordance with the methods used to develop the NPZ model, the focus of this new analysis is on three zooplankton groups (copepods, euphausiids, all other zooplankton grouped as "spring" zooplankton). As noted in the report titled "Hecate Strait Climate-Forced Nutrient, Phytoplankton, Zooplankton Model Version 4.3.4" (Ware and McQueen, 2006), the field data (combined over all years) showed that zooplankton other than copepods and euphausiids (called "spring" or "other" zooplankton) peaked in the spring, followed by copepods, which peaked in the summer, and euphausiids in the fall. This pattern is clearly seen in Figure 17, as well as in Figures 23 and 24 from Ware and McQueen (2006).

Having established that the three zooplankton groups show distinct seasonal patterns, the next step was to ask whether the field data reveal significant interannual abundance patterns for the three zooplankton groups. The answer appears to be that the three groups do have quite different abundances in different years (Fig. 18). The "spring" zooplankton are about equally abundant throughout the data set (1990–2002), copepods appeared to be more abundant during the mid-1990s, and euphausiids were more abundant in the late 1990s and early 2000s. As was the case with the earlier data set (used in McQueen and Ware 2006), there is a positive relationship between the individual daily values for copepods plotted with respect to euphausiids. This indicates that both groups tend to increase together (Fig. 19), perhaps in response to bottom-up changes in the environment.

However, these patterns must be treated with caution! Comparisons between the interannual zooplankton patterns produced by the NPZ model and the interannual patterns noted above (Fig. 18) require reasonably small confidence intervals for the field data. This appears not to be the case (Fig. 20). In almost all cases, ± 1 standard deviation on the mean overlaps zero. Briefly stated, the between-sample variability is so high that apparent interannual differences cannot be statistically resolved with the existing data. *The implication is that attempts to compare interannual changes in model output with the existing field data will not provide a meaningful test of the model, and therefore should not be attempted.*

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Table 1. Sources of nitrogen input (cumulative mg $N \cdot m^{-3}$) to the Hecate Strait/Queen Charlotte Sound Region 1991-99. Model v4.3.4.

Year	New Nitrogen				Regenerated Nitrogen
	Winter Mixing	Seasonal Mixing	Upwelling	Total	
1991	280	**509**	336	1125	229
1992	280	146	**462**	888	189
1993	280	294	**480**	1054	220
1994	280	**260**	**273**	813	152
1995	280	248	**313**	841	211
1996	280	**349**	289	918	168
1997	280	**419**	208	907	198
1998	280	85	**480**	845	191
1999	280	**460**	220	960	179

Table 2. Number of major wind mixing events during the spring bloom, estimated date when the spring bloom peaked, and cumulative proportion of the primary production grazed by zooplankton (ecotrophic coefficient).

Year	Number of Major Mixing Events	Bloom Peak	Fraction Grazed
1991	4	April 29	0.47
1992	0	March 9	0.53
1993	3	May 1	0.52
1994	2	March 30	0.50
1995	3	April 27	0.53
1996	3	March 28	0.50
1997	5	April 24	0.50
1998	0	March 12	0.53
1999	5	May 5	0.44

Table 3. Seasonal averages of climate data (March 1 to Nov. 30) around Buoy 46185 (in northern Queen Charlotte Sound) and lower trophic level production estimates for 1991-1999. CF-NPZ co-lim **Model v4.3.3**.

Average	1991	1992	1993	1994	1995	1996	1997	1998	1999
SST (°C)	10.95	11.69	11.62	11.54	11.58	11.04	12.08	12.21	*10.50*
Sunlight (hrs)	4.93	4.78	4.47	4.47	4.78	4.89	5.07	5.10	*4.14*
A-Wind ($m \cdot s^{-1}$)	4.86	4.97	4.81	*4.40*	4.47	4.80	4.80	4.57	5.14
Upwelling-Wind ($m \cdot s^{-1}$)	2.06	2.41	2.49	1.81	1.91	1.78	1.28	2.61	*1.55*
Delta-SST (°C)	4.95	5.69	5.62	5.54	5.58	5.04	6.08	6.21	*4.50*
Mixing depth (m)	16.97	12.7	14.79	12.39	13.39	15.66	15.94	*10.40*	17.40
f-ratio	0.72	0.73	0.77	0.71	0.69	0.72	0.68	0.72	0.71
Sedimentation /Net PP	0.15	0.13	0.19	0.14	0.12	0.15	0.16	0.12	0.20
Phytoplankton									
Net production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	130.6	168.3	165.6	124.6	133.5	125.1	108.0	184.1	106.5
Mean B ($g\ C \cdot m^{-2}$)	13.2	13.2	12.7	11.3	11.3	12.17	10.76	12.0	11.8
P/B_{net} (yr^{-1})	9.9	12.8	13.0	11.0	11.8	10.3	10.0	15.4	9.0
"Spring" Zooplankton									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	13.0	16.8	11.3	12.8	16.03	12.12	11.58	22.1	9.73
B ($g\ C \cdot m^{-2}$)	0.94	1.23	0.86	0.98	1.12	0.93	0.89	1.59	0.79
P/B (yr^{-1})	13.8	13.7	13.1	13.1	14.3	13.0	13.0	13.9	12.3
Copepods									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	2.45	2.65	2.63	1.63	2.01	1.91	1.15	1.84	1.58
B ($g\ C \cdot m^{-2}$)	0.12	0.13	0.13	0.09	0.11	0.10	0.07	0.10	0.09
P/B (yr^{-1})	20.0	20.5	20.2	18.1	18.3	19.1	16.4	18.4	17.6
Euphausiids									
Production($g\ C \cdot m^{-2} \cdot yr^{-1}$)	4.67	6.08	8.17	2.92	3.29	3.41	2.33	4.17	2.62
B ($g\ C \cdot m^{-2}$)	0.26	0.32	0.40	0.17	0.20	0.19	0.13	0.22	0.14
P/B (yr^{-1})	18.0	19.0	20.4	17.2	16.5	17.9	17.9	18.9	18.7
Total Zooplankton									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	20.2	25.5	22.1	17.4	21.3	17.44	15.1	28.1	13.9
Transfer Efficiency	0.15	0.15	0.13	0.14	0.16	0.14	0.14	0.15	0.13

Table 4. Seasonal averages of climate data (March 1 to Nov. 30) around Buoy 46185 (in northern Queen Charlotte Sound) and lower trophic level production estimates for 1991-1999. CF-NPZ co-lim **Model v4.3.4** (Wind mixing and Upwelling).

Average	1991	1992	1993	1994	1995	1996	1997	1998	1999
SST (°C)	10.95	11.69	11.62	11.54	11.58	11.04	12.08	12.21	10.50
Sunlight (hrs)	4.93	4.78	4.47	4.47	4.78	4.89	5.07	5.10	4.14
A-Wind ($m \cdot s^{-1}$)	4.86	4.97	4.81	4.40	4.47	4.80	4.80	4.57	5.14
Upwelling-Wind ($m \cdot s^{-1}$)	2.06	2.41	2.49	1.81	1.91	1.78	1.28	2.61	1.55
Delta-SST (°C)	4.95	5.69	5.62	5.54	5.58	5.04	6.08	6.21	4.50
Mixing depth (m)	16.97	12.7	14.79	12.39	13.39	15.66	15.94	10.40	17.40
f-ratio	0.83	0.82	0.83	0.84	0.80	0.84	0.82	0.82	0.84
Sedimentation /Net PP	0.19	0.14	0.14	0.15	0.14	0.16	0.17	0.12	0.21
Phytoplankton									
Net production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	189.7	192.9	207.0	153.9	175.7	160.8	170.0	202.3	169.8
Mean B ($g\ C \cdot m^{-2}$)	18.1	14.5	14.9	13.9	14.6	15.3	14.5	12.9	17.6
P/B_{net} (yr^{-1})	10.4	13.3	13.9	11.1	12.0	10.5	11.7	15.7	9.6
"Spring" Zooplankton									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	18.8	19.6	18.7	18.1	23.3	17.91	22.8	23.0	15.0
B ($g\ C \cdot m^{-2}$)	1.18	1.37	1.19	1.25	1.43	1.22	1.38	1.64	1.02
P/B (yr^{-1})	15.9	14.3	15.7	14.5	16.3	14.7	16.5	14.0	14.7
Copepods									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	5.38	2.64	3.54	1.94	3.57	2.79	3.03	1.83	3.99
B ($g\ C \cdot m^{-2}$)	0.23	0.13	0.16	0.10	0.16	0.14	0.14	0.10	0.18
P/B (yr^{-1})	23.4	20.6	22.1	19.4	22.3	19.9	21.6	18.3	22.2
Euphausiids									
Production($g\ C \cdot m^{-2} \cdot yr^{-1}$)	11.0	6.7	11.5	3.2	5.51	5.0	4.6	4.4	8.3
B ($g\ C \cdot m^{-2}$)	0.59	0.34	0.60	0.19	0.34	0.28	0.30	0.23	0.42
P/B (yr^{-1})	18.6	19.3	19.2	16.8	16.2	17.9	15.3	19.1	19.8
Total Zooplankton									
Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	35.2	28.9	33.7	23.3	32.4	25.7	30.4	29.2	27.4
Transfer Efficiency	0.18	0.15	0.16	0.15	0.18	0.16	0.18	0.14	0.16

Table 5. Average monthly surface chlorophyll *a* concentration estimated by the SeaWiFS satellite and by Models v4.3.3 and v4.3.4.

Year	Month	Average monthly surface chl *a* ($mg \cdot m^{-3}$)		
		SeaWiFS	Model v4.3.3	Model v4.3.4
1998	3	2.35	6.53	6.71
1998	4	6.59	7.85	8.25
1998	5	2.16	6.18	6.46
1998	6	2.04	2.61	2.81
1998	7	3.19	1.34	1.35
1998	8	3.15	2.49	2.44
1998	9	3.20	2.13	2.07
1999	3	1.77	4.87	5.05
1999	4	2.37	7.33	8.31
1999	5	4.10	5.53	13.48
1999	6	3.89	3.21	11.06
1999	7	2.51	2.38	8.44
1999	8	2.02	3.12	8.53
1999	9	3.62	2.36	5.45

Table 6. Estimates of copepod production, the calendar day when the spring bloom peaked, and the growth rate anomaly of Cassin's auklet nestlings.

Year	v4.3.3 Copepod production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	v4.3.4 Copepod production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	v4.3.4 Spring bloom peak (Day)	Cassin's auklet growth rate anomaly ($g \cdot d^{-1}$)
1991	2.45	5.38	119	.
1992	2.65	2.64	68	.
1993	2.63	3.54	121	.
1994	1.63	1.94	89	-0.1
1995	2.01	3.57	117	-0.7
1996	1.91	2.78	87	-2.0
1997	1.15	3.04	114	-0.6
1998	1.84	1.83	71	-0.5
1999	1.58	3.99	125	2.0

Table 7. Average annual population specific growth (PSG) rates of Central Coast (CC), Queen Charlotte Islands (QCI) and Prince Rupert District (PRD) Pacific herring populations for 1991-1998.

Year	CC PSG	QCI PSG	PRD PSG
1991	1.465	1.426	1.470
1992	1.493	1.433	1.425
1993	1.506	1.630	1.521
1994	1.527	1.339	1.532
1995	1.369	1.467	1.408
1996	1.426	1.264	1.360
1997	1.506	1.597	1.654
1998	1.569	1.431	1.358

Table 8. Correlation between the growth rates of the Central Coast (CC), Queen Charlotte Islands (QCI) and Prince Rupert District (PRD) herring populations, and the primary and zooplankton production rates (g $C \cdot m^{-2} \cdot yr^{-1}$) estimated by Model v4.3.3 (first number in each column) and Model v4.3.4 (bracketed number in each column).

Variable	Primary Production	"Spring" Zooplankton Production	Copepod Production	Euphausiid Production
CC PSG	0.43 [0.32]	0.30 [-0.23]	-0.14 [-0.47]	0.18 [-0.10]
QCI PSG	0.14 [**0.54**]	0.06 [**0.65**]	0.06 [**0.26**]	0.41 [**0.45**]
PRD PSG	-0.51 [-0.20]	-0.61 [0.10]	-0.40 [0.14]	-0.11 [0.07]

Table 9. Estimated annual average alongshore wind speed (Mean A-Wind), average upwelling-favourable (i.e. northerly) wind speed (Mean UWind), number of days when winds were upwelling-favourable, cumulative upwelling wind (Cumulative UWind), and annual primary production estimates based on Mean UWind speed. All annual estimates are for the period 1 March to 30 November.

Year	Mean A-Wind ($m \cdot s^{-1}$)	Mean UWind ($m \cdot s^{-1}$)	Upwelling Days	Cumulative UWind ($m \cdot s^{-1}$)	Est. Primary Production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)
2002	4.15	2.02	143	556	190
2001	4.21	1.57	127	430	168
2000	4.21	1.80	147	494	179
1999	5.30	1.79	138	493	179
1998	4.17	2.02	155	555	190
1997	4.05	1.26	98	346	153
1996	4.03	1.74	140	478	177
1995	3.98	1.86	147	511	182
1994	3.56	1.73	148	477	176
1993	4.01	1.97	159	540	188
1992	4.02	2.00	160	550	189
1991	3.80	1.97	157	541	188
1990	3.95	1.85	144	501	182
1989	3.55	1.71	147	471	175
1988	3.72	1.38	130	377	159
1987	4.25	1.66	137	455	173
1986	4.15	1.82	149	500	180
1985	3.46	2.04	171	561	191
1984	4.26	1.13	110	310	147
1983	3.71	1.38	132	378	159
1982	3.64	2.05	174	564	192
1981	4.12	1.45	119	398	162
1980	4.19	2.02	150	556	190

Table 10. Average biomass of various zooplankton in Hecate Strait and Queen Charlotte Sound. The estimates are based on 244 samples.

Functional Group	Average biomass ($mg(dry) \cdot m^{-3}$)
Copepods	
Small copepods	5.56
Medium copepods	9.18
Large copepods	1.55
Total	**16.29**
Euphausiids	
Euphausiia	3.88
Thysanoessa	11.74
Total	**15.62**
"Spring" Zooplankton	
Pteropods (*Limacina*)	17.85
Other zooplankton	9.82
Coelenterates (Medusae)	4.22
Barnacle larvae	2.61
Chaetognatha	1.38
Urochordates (salps)	0.74
Bryzoans	0.38
Amphipods	0.18
Ctenophores	0.18
Coelenterates	0.11
Polychaetes	0.06
Cladocerans	0.04
Total	**37.61**
Grand Total	**69.52**

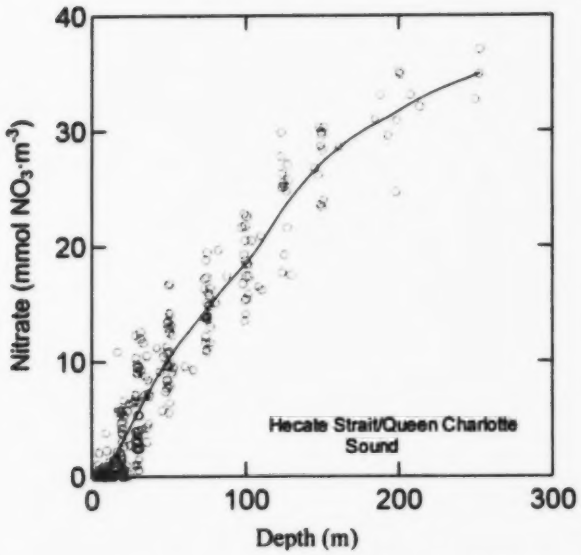

Figure 1. Nitrate concentration (mmol $NO_3 \cdot m^{-3}$) at depth for June/July 1983. Source: *Denman et al (1985).*

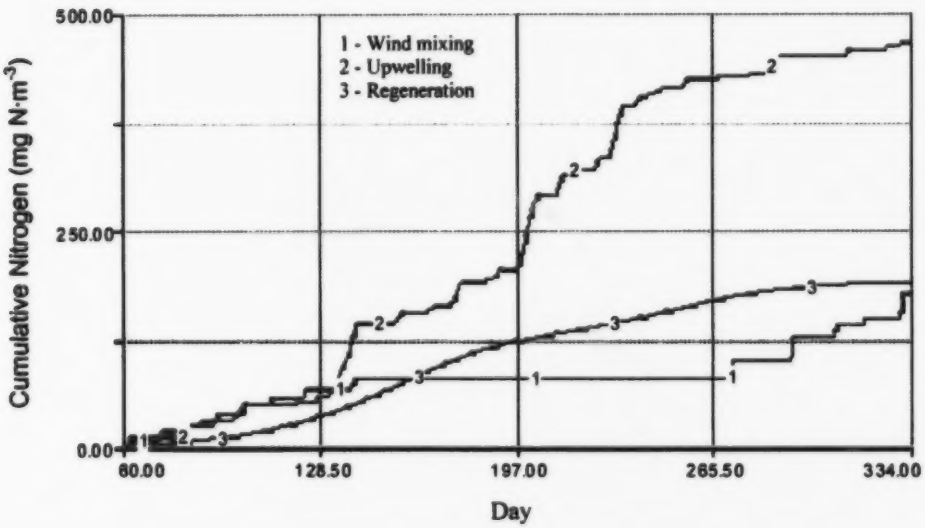

Figure 2. Estimated cumulative input of nitrogen (mg $N \cdot m^{-3}$) to the photic zone in 1992 by: 1) wind mixing, 2) upwelling, and 3) regeneration processes. Note that Day 60 is 1 March and Day 334 is 30 November.

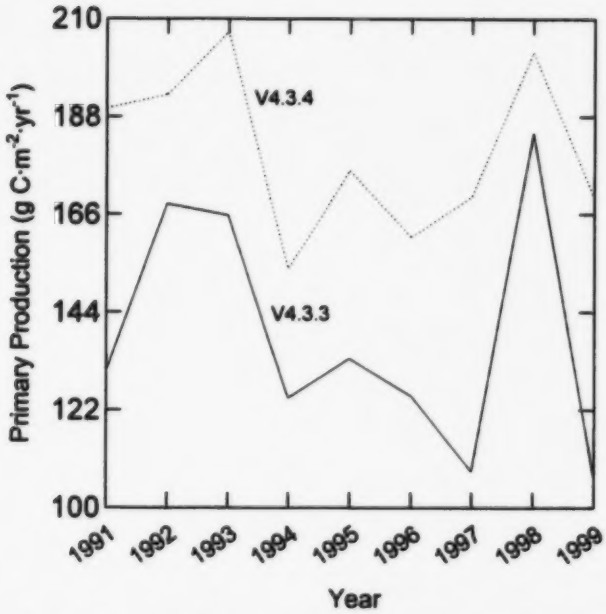

Figure 3. Model v4.3.3 and v4.3.4 estimates of primary production (g $C \cdot m^{-2} \cdot yr^{-1}$).

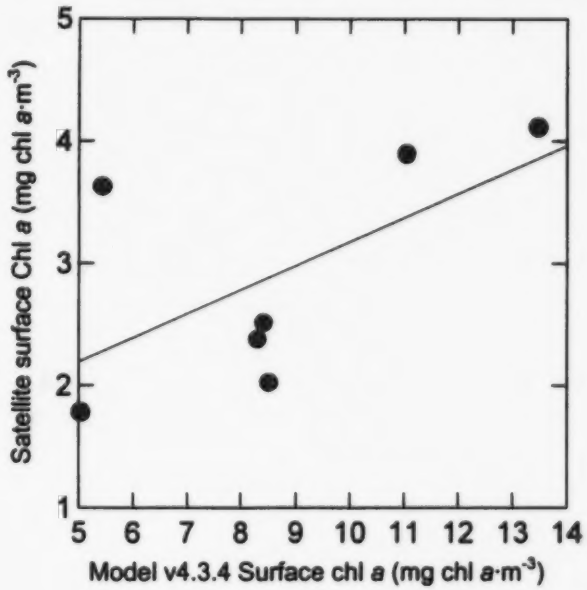

Figure 4. Surface concentration of chlorophyll *a* (mg chl $a \cdot m^{-3}$) estimated by the SeaWiFS satellite and by Model v4.3.4. Note that the difference in the magnitude of the two estimates is simply a scaling issue. The model estimates can be scaled down to match the satellite estimates.

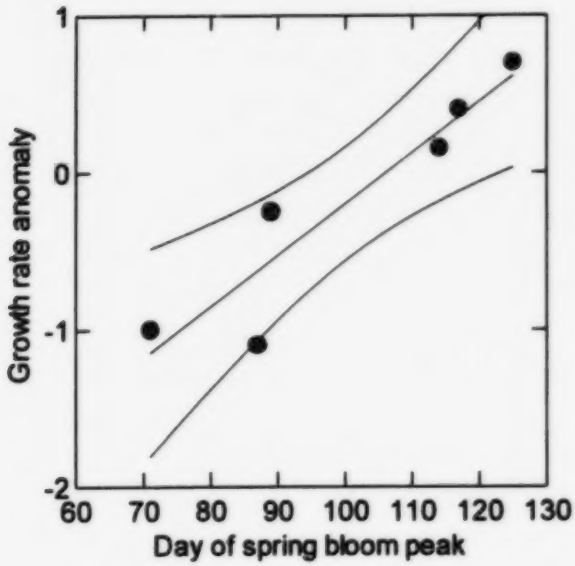

Figure 5. Relationship between the growth rate anomalies ($g \cdot d^{-1}$) of Cassin's auklet nestlings and the calendar day when the spring bloom peaked in Model v4.3.4. $n = 6$; $r^2 = 0.86$; $p = 0.007$. The 90% confidence limits of the regression are shown. Source: *Bertram et al (2001)*.

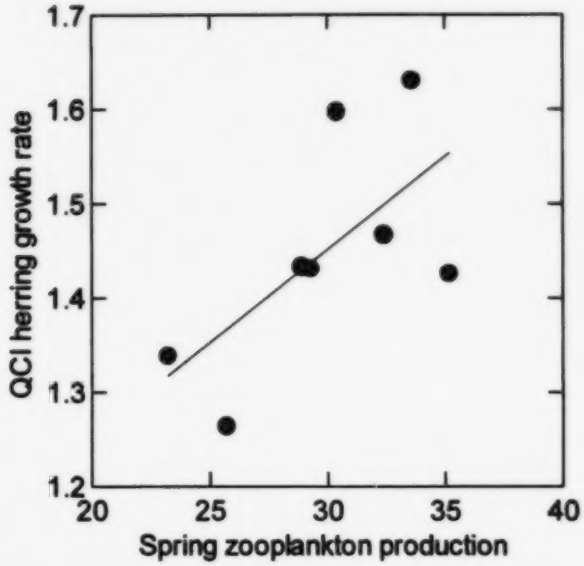

Figure 6. Relationship between Queen Charlotte Islands (QCI) herring growth rates and the production of "spring" zooplankton ($g\ C \cdot m^{-2} \cdot yr^{-1}$) from 1991 to 1998. $n = 8$; $r^2 = 0.42$; $p = 0.08$. Source: *DFO herring database*.

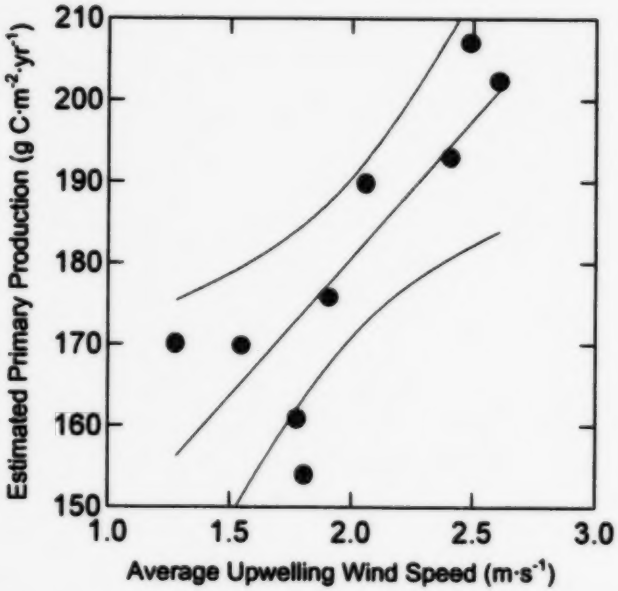

Figure 7. Primary production (g $C \cdot m^{-2} \cdot yr^{-1}$) estimated by Model v4.3.4 with respect to the average speed of upwelling-favourable winds at Buoy 46185 from 1991-1999. $n = 9$; $r^2 = 0.67$; $p = 0.007$. The 90% confidence limits on the regression are shown.

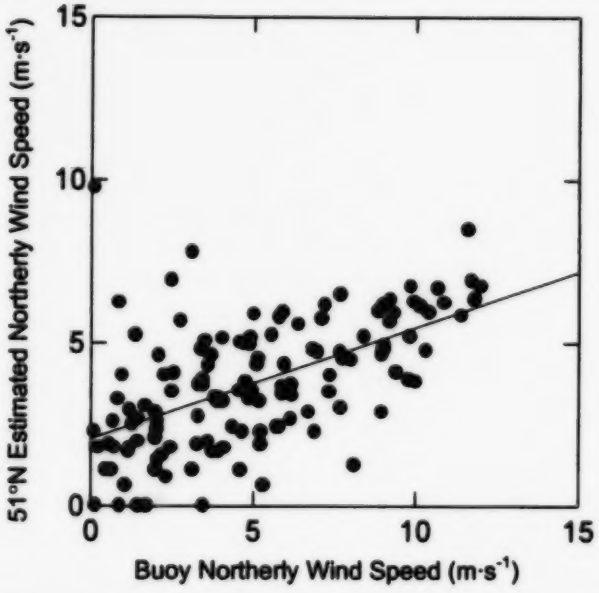

Figure 8. Relationship between upwelling-favourable northerly wind speeds at Buoy 46185 and at 51°N 131°W in 1992. $n = 177$; $r^2 = 0.29$; $p < 0.0001$.

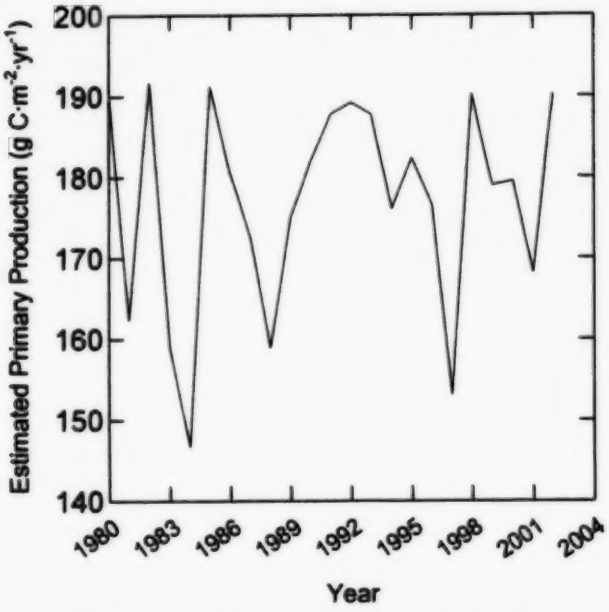

Figure 9. Estimated primary production in the Hecate Strait Region for 1980-2002. Note that the most productive years were 1980, 1982, 1985, 1992, 1998 and 2002. The least productive years were 1983, 1984, 1988, and 1997.

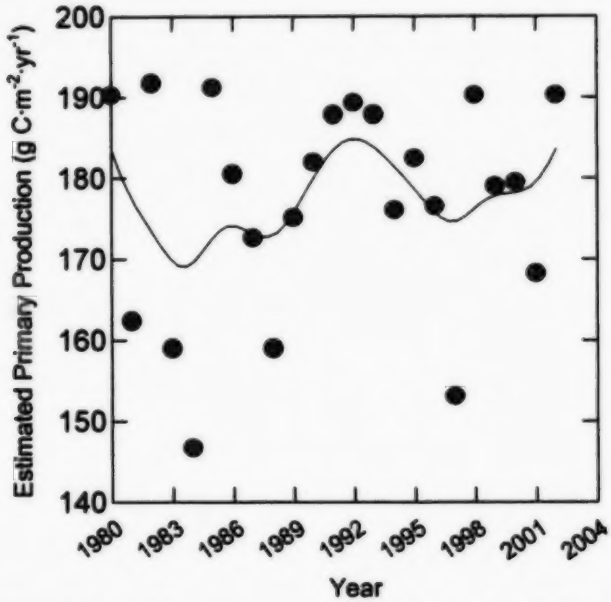

Figure 10. Decadal trend in primary production (g $C \cdot m^{-2} \cdot yr^{-1}$) for 1980-2002.

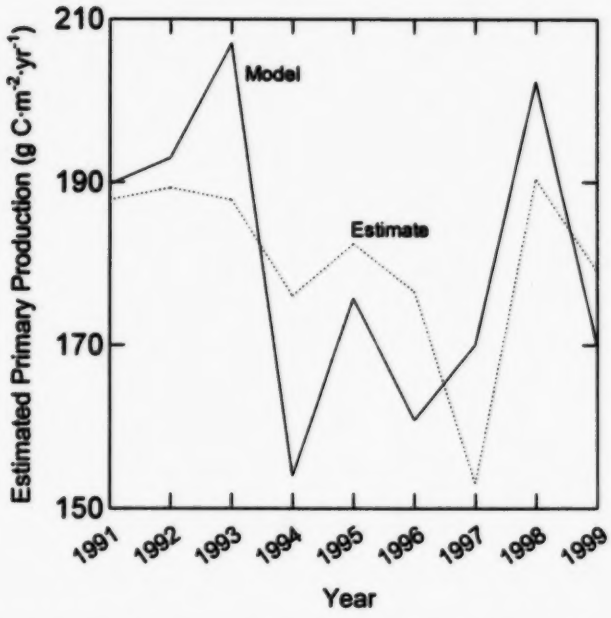

Figure 11. Comparison of the annual primary production estimated by Model v4.3.4 and by the proxy upwelling time series at 51°N 131°W (curve labeled "estimate"). n = 9; $r^2 = 0.40$; p = 0.07.

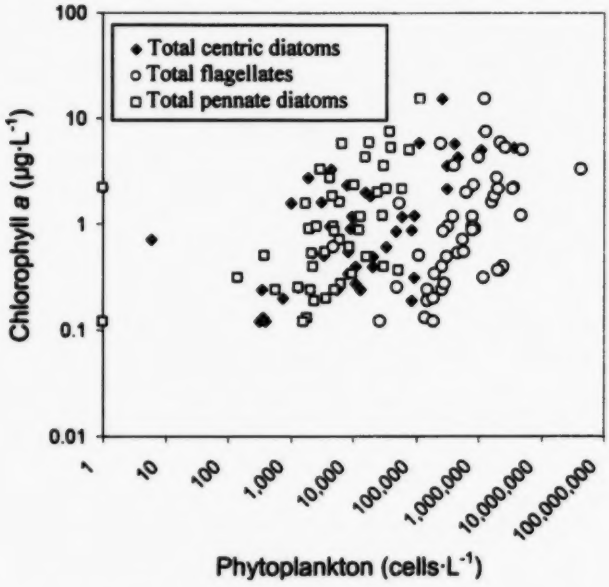

Figure 12. Relationship between chlorophyll *a* and phytoplankton cell counts.

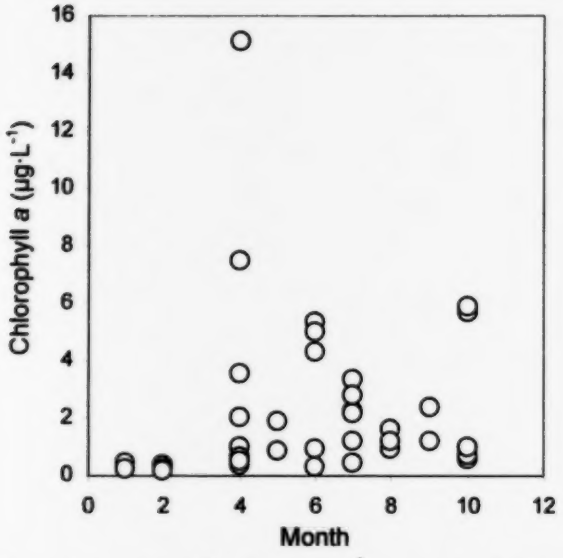

Figure 13. Chlorophyll *a* ($\mu g \cdot L^{-1}$) with respect to month of the year.

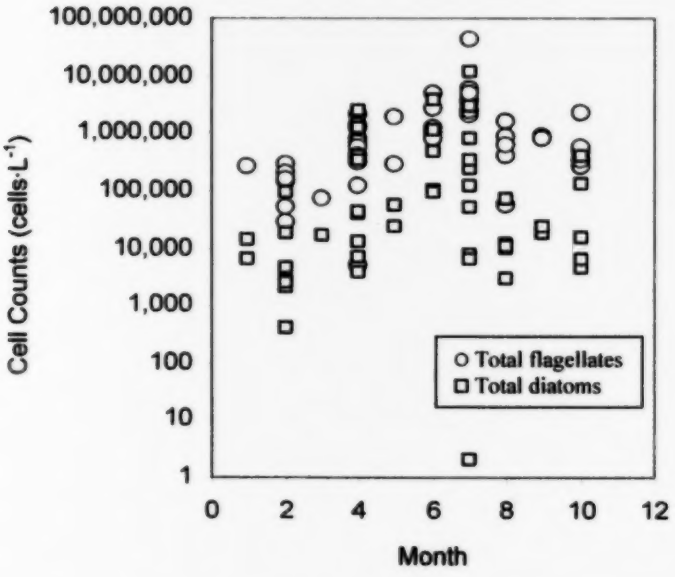

Figure 14. Cell counts of total flagellates and total diatoms with respect to the month of the year.

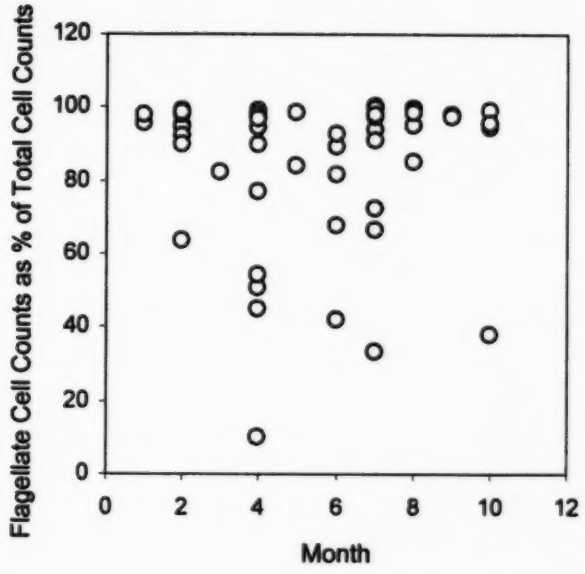

Figure 15. Monthly pattern for total flagellates expressed as a percentage of total cell counts.

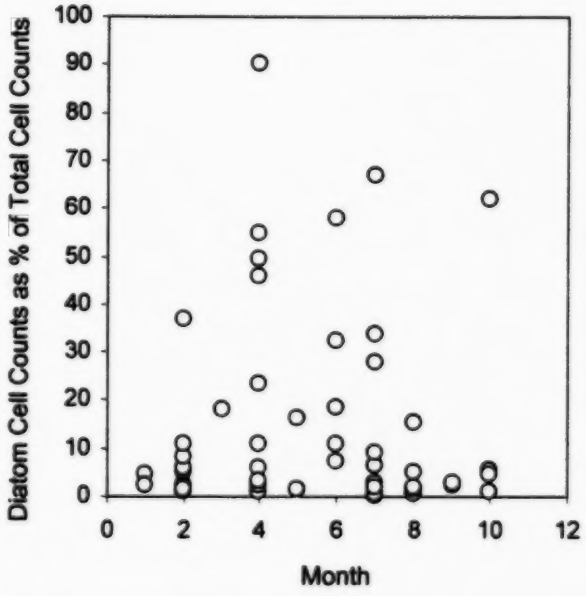

Figure 16. Monthly pattern for total diatoms expressed as a percentage of total cell counts.

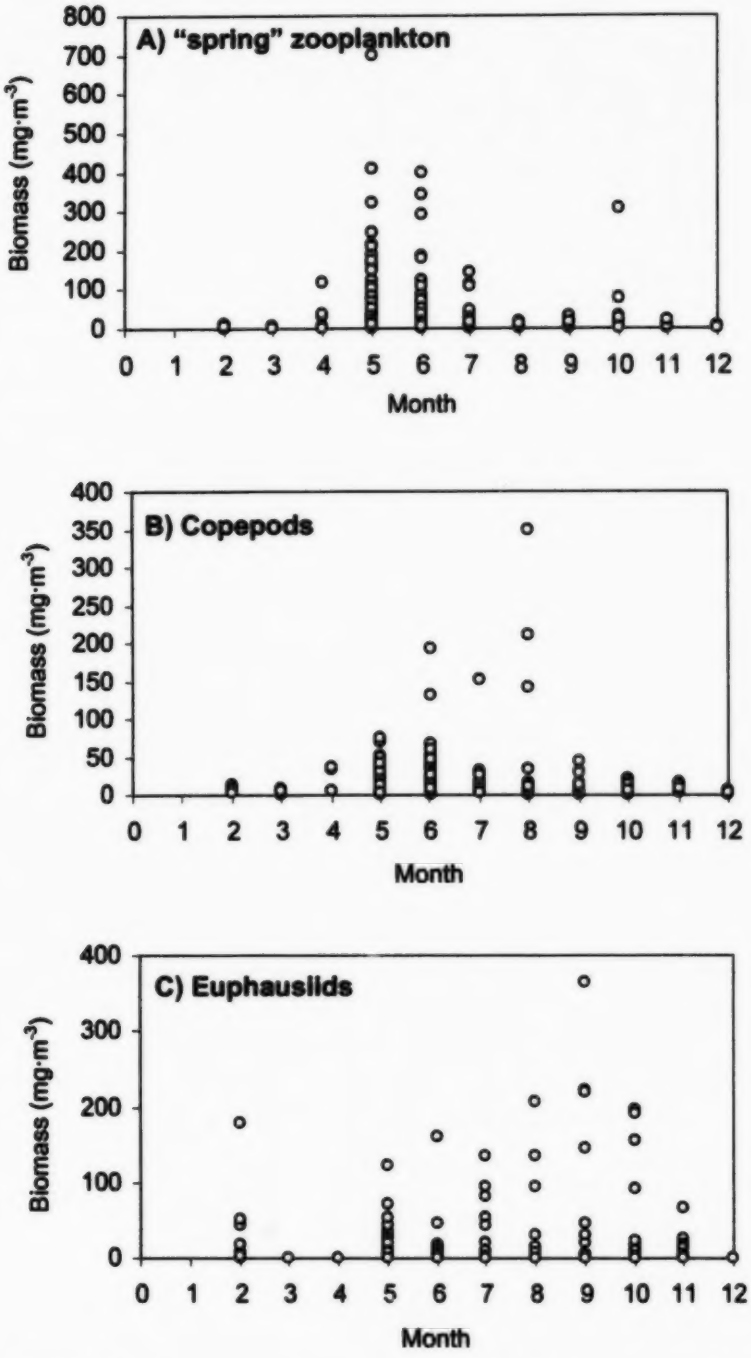

Figure 17. Monthly biomasses of: A) "spring" zooplankton, B) copepods, and C) euphausiids.

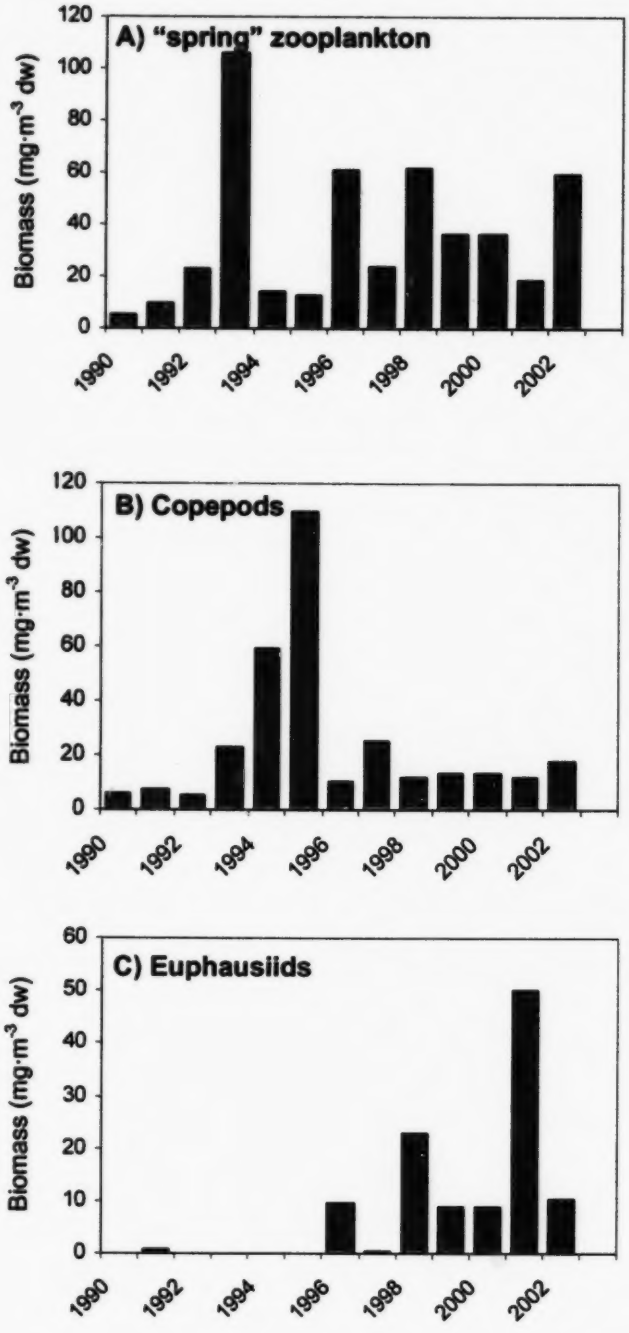

Figure 18. Interannual patterns in the field data for: A) "spring" zooplankton, B) copepods, and C) euphausiids.

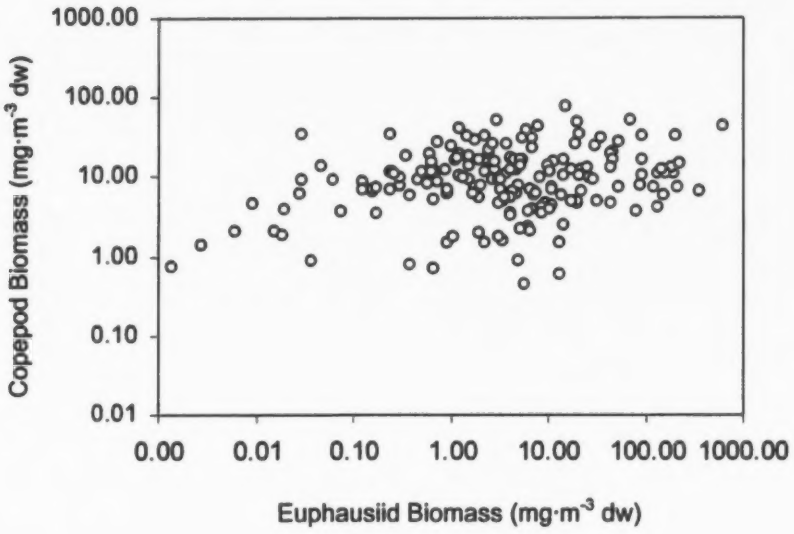

Figure 19. Copepod biomass ($mg \cdot m^{-3}$ dry weight) with respect to euphausiid biomass. All data from 1990 to 2002 are included.

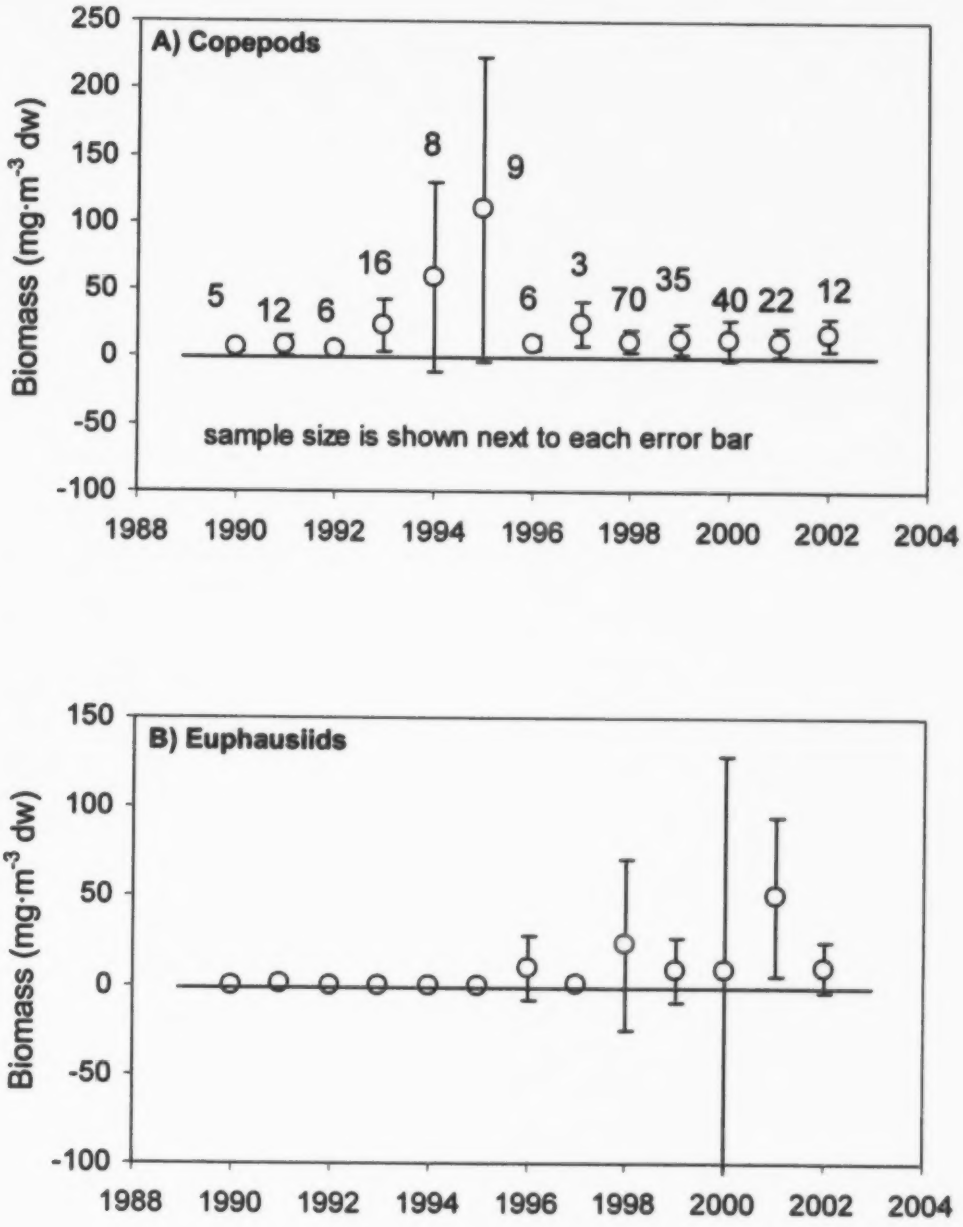

Figure 20. Mean annual biomass estimates ±1 standard deviation for: A) copepods and B) euphausiids. Annual sample sizes are shown beside each mean plotted in panel A.

APPENDICES

Appendix A: Conversion Factors

Nutrient, Phytoplankton, Zooplankton Model Output

- Raw model units of biomass are g $C \cdot m^{-3}$
- Model units are converted to **g $C \cdot m^{-2}$** by multiplying g $C \cdot m^{-3}$ by the depth of the photic zone (about 30 m).
- To convert **g $C \cdot m^{-2}$** to **tonnes(wet)$\cdot km^{-2}$** we use the following ratios:
  - Phytoplankton (Various sources)
    Carbon/dry wt = 0.5
    Dry/wet wt = 0.15
    Thus, tonnes(wet)$\cdot km^{-2}$ = 1/(0.5*0.15) = **13.3 x g $C \cdot m^{-2}$**

  - Copepods and "spring" Zooplankton (Omori 1969)
    Carbon/dry wt = 0.52
    Dry/wet wt = 0.216
    Thus, tonnes(wet)$\cdot km^{-2}$ = 1/(0.52*0.216) = **8.9 x g $C \cdot m^{-2}$**

  - Euphausiids (Various Sources)
    Carbon/dry wt = 0.43
    Dry/wet wt = 0.207
    Thus, tonnes(wet)$\cdot km^{-2}$ = 1/(0.43*0.207) = **11.2 x g $C \cdot m^{-2}$**

Hecate Strait Plankton Sample Data

- raw units = **mg(dry)$\cdot m^{-3}$**
- Note that **1 tonne$\cdot km^{-2}$ = 1 g$\cdot m^{-2}$**
- The average haul depth for the plankton samples collected in Hecate Strait/Queen Charlotte Sound that we analyzed was **107 m**.
- To convert to **tonnes$\cdot km^{2}$**:
  Divide mg(dry)$\cdot m^{-3}$ by dry/wet ratio = 0.17
  Multiply by haul depth = 107 m
  Divide by 1000 to convert mg(wet) to g(wet)
  Answer has units of = g$\cdot m^{-2}$ or tonnes$\cdot km^{-2}$

  Example: 2.6 mg(dry)$\cdot m^{-3}$ = [(2.6/0.17) x 107 /1000] = 1.64 g$\cdot m^{-2}$ or tonnes$\cdot km^{-2}$.
  2.6 mg(dry)$\cdot m^{-3}$ = **0.6294***2.6 mg(dry)$\cdot m^{-3}$ = 1.64 g$\cdot m^{-2}$ or tonnes$\cdot km^{-2}$.

Reference:

Omori, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. 3: 4-10.

Appendix B: Reference List of Excel Data Files Available via Download

Electronic versions of this report ("*TR2654 Hecate Retrospectives.pdf*") and the following Excel spreadsheets will soon be available by searching the Fisheries and Oceans Canada "Waves" library (http://inter01.dfo-mpo.gc.ca/waves2/search.html) online for this report. Once your search locates the report, choose "View Online" from the DFO Internet Copy near the bottom left of the web page to then select the files you wish to download. All three data files may be downloaded at once by selecting the zip file "*TR2654 Retrospectives Data.zip*".

File Name	Contents	See Page #
Dilke et al 1979 chla phyto.xls	Chlorophyll and phytoplankton data from Dilke *et al* (1979)	6
Perry et al 1981 chla phyto.xls	Chlorophyll and phytoplankton data from Perry *et al* (1981)	6
Zooplankton Hecate QCS.xls	Updated zooplankton data set for Hecate Strait and Queen Charlotte Sound that includes samples from 1990 to 2002	8
TR2654 Hecate Retrospectives.pdf	PDF version of this document	